# EXPERIMENTAL STUDIES ON VISION IN INDIAN SNAKES[1]

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(*With a text-figure*)

In about 300 specimens of 10 species of Indian snakes, the visual acuity was tested by optomotor reactions. 6 species yielded results ranging from 4′30″ (angular degrees) in the ratsnake (*Ptyas mucosus*) to 1°15′ in the dog-faced watersnake (*Cerberus rhynchops*). An intermediate visual acuity is represented by the saw-scaled viper (*Echis carinatus*), with 12 angular minutes reaching the visual acuity of the European lizard *Lacerta agilis*. On the contrary, the Cobra (*Naja naja*) with 5′30″ has a definitely better vision than the lizard. Surprisingly, the Indian Python did not show any optomotor reactions at all.

Vision can be assessed by studying brightness discrimination and colour perception or by quantifying the visual acuity. The latter is the most important factor determining the quality of visual information of an individual. Moreover, visual acuity is a favourable means of comparing 'vision' in various animal species, and, of course, in man.

Visual acuity can be determined by at least three methods: i. by histological measurements, i.e. assessing the angle between the optical axes of two neighbouring retinal elements; ii. by using optomotor reactions of the experimental animal in a revolving black-white striped drum; iii. by classical conditioning, i.e. making the animal respond to one of two black-white striped visual discriminanda.

The data obtained by method i. are referred to as morphological visual acuity, while methods ii. and iii. would yield the physiological visual acuity. These methods will be dealt with in more detail later on. For a survey of findings on the visual acuity in mammals and birds is presented in the Table 1.

Unfortunately, and in contrast to the list in Table 1, corresponding studies in reptiles, amphibians and fishes are scanty. This can be seen from Table 2.

It must be mentioned here, that the term 'minimum separabile' denotes the narrowest black-white striped pattern resolved by the test animal in the optomotor or conditioning situation.

Visual acuity is limited by various factors, of which the following are most important: It is obvious, that vision in its broadest sense is determined by the structure of the retina, i.e., the diameter of retinal receptors and their spatial density (as number per square unit). Apart from this geometrical aspect, visual acuity is also affected by the number of receptors per ganglionic cell. Obviously, this ratio is at best 1:1, which means, that each visual receptor has its own separate ganglionic connection to the brain (Walls 1942).

Such favourable ratios are only found in the area centralis, and hence, here visual performance is optimal. Towards the periphery of the retina this ratio is definitely inferior, here many

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TABLE 1

VISUAL ACUITY IN MAMMALS AND BIRDS

| Species | Visual acuity | Author |
|---|---|---|
| man | 20″ | Loevenich 1949 |
| chimpanzee | 28″ | Spence 1934 |
| Indian elephant | 10′20″ | Altevogt 1955 |
| dwarfgoat | 9′36″ | Backhaus 1959 |
| donkey | 8′36″ | Backhaus 1959 |
| cat | 5′30″ | Smith 1936 |
| bats | 5°–3° | Suthers 1966 |
| deermice | 1°34′–33′ | Rahmann *et al.* 1968 |
| chinchilla | 30′ | Thomas 1964 |
| Indian vulture | 13′3″ | Fischer 1969 |
| white scavenger vulture | 13′3″ | Fischer 1969 |
| budgerigar | 28″ | Kurze 1976 |
| blackbird | 1′20″ | Donner 1951 |
| robin | 2′38″ | Donner 1951 |
| yellow bunting | 3′07″ | Donner 1951 |

TABLE 2

| Species | Visual acuity as minimum separabile | Author |
|---|---|---|
| minnow | 11′ | Brunner 1935 |
| cichlid fish | 5′30″ | Baerends and coworkers 1960 |
| common carp | 16′ | Zimmer 1966 |
| frog | 6′53″ | Birukow 1938 |
| lizard | 11′28″ | Ehrenhardt 1937 |
| tortoise | 5′30″ | Dudziak 1956 |

receptor cells are switched to only one ganglionic pathway. Not all animal eyes studied attain the 1:1 ratio.

For geometrical reasons, the quality of the retinal image is also determined by shape and size of the lens. Clearly, accommodation comes about by altering focal length. From geometrical considerations it becomes clear, that the retinal image depends also on the size of the eye, and generally, a larger eye is more efficient than a smaller one (Von Buddenbrock 1952). This was found in man, where the average adult visual acuity according to Spence (1934) amounts to 26″ while in

Infants it averages only 37″.

A similar finding by Baerends and coworkers (1960) refers to adult and juvenile fishes (*Aequidens portalegrensis*): 10-11 cm long adults averaged 5′-30′, youngsters scored only 44′32″.

From personal experience everybody knows that visual acuity strongly depends on environmental brightness. Apart from this well-known fact in humans this has been shown in a number of animals also (see: Brunner 1935, Ehrenhardt 1937, Birukow 1938, Donner 1951, Altevogt 1955, Kurze 1976, and others).

Corresponding to retinal brightness the size of receptive retinal areas varies and is smallest at optimal brightness level. Under such conditions the 1:1 ratio of retinal and ganglionic elements is obtained, and visual performance is best (Kuffler 1952, Kuffler and coworkers 1957, and Granit 1955 and 1957).

As mentioned above, visual acuity can also be quantified by methods of classical conditioning, i.e. training the test animal to choose the finer striped pattern versus the coarse striped one.

Apart from the experimental methods mentioned, one can also obtain information on the visual acuity of an animal by observations in the field. Thus, one can calculate the visual acuity from the distance from which a prey of a certain size (say a mouse) is spotted by an animal (say a bustard). In this manner Schuyl and Tinbergen (1936) measured the visual acuity of the Peregrine falcon (*Falco subbuteo*) as 21″ (from Fischer 1969). Similarly, Ehrenhardt (1937) offered a mealworm at a distance of 95 cm from a lizard (*Lacerta vivipara*) and saw, that the test animal spotted the prey from this distance guided exclusively by visual clues. The visual acuity under these conditions amounted to 14′38″.

The conditioning method mentioned above can successfully be applied only in animals of sufficient learning capacity. According to common belief, snakes do not seem to be gifted learners, so that classical conditioning seems unfeasible.

Therefore I turned to using optomotor reactions by placing the test animal in the centre of a revolving drum featuring vertical aequidistant black-white stripes, the dimensions of which could be varied. The animal reflectorily tries to keep its visual field constant by following the moving stripes with eyes, head or body movements. These efforts result in jerkwise movements in correlation with rotation speed, and size and number of black and white stripes. From Ehrenhardt's studies (1937) we have the first records of visual acuity in the European lizard species *Lacerta agilis* (Table 2).

From the above remarks and facts mentioned, it seems appropriate that for the determination of visual acuity in snakes the optomotor method should be applied. In captivity, snakes are rather delicate animals, sometimes refusing food for weeks and months. Optomotor reactions, however, remain independent of rearing conditions. Thus, they yield reliable data. Thanks to the favourable opportunities offered by the Madras Snake Park and my laboratory facilities in the Zoological Institute in Münster University I could work on about 300 Indian snakes belonging to 10 species.

In the Madras Snake Park the animals lived under nearly natural habitats though under slightly crowded conditions. They were given frogs and mice in sufficient numbers. In the Münster laboratory, the animals were housed in large terraria at temperatures between 25° C and 28° C, the relative humidity ranging from 40 to 70%. Baby mice and frogs were given as food.

The optomotor apparatus is shown in fig. 1 from which also the relevant dimensions can be seen. The revolving drum was first equipped with vertical stripes of 35 cm, equalling 20 angular degrees. If this pattern evoked optomotor reactions in the test animal, I would reduce the width of the stripes by half, i.e. to 17.5 cm, equalling 10°. By further reducing the width I was able to provide visual angles of 5°, 2.5°, 1°15′, 17′, 5′57″. As it proved difficult to precisely cut black paper stripes of less than 5 mm width, equalling 17′, I finally used precisely striped cloth, the dark brown and white stripes being 1.73 mm wide each, equalling 5′57″.

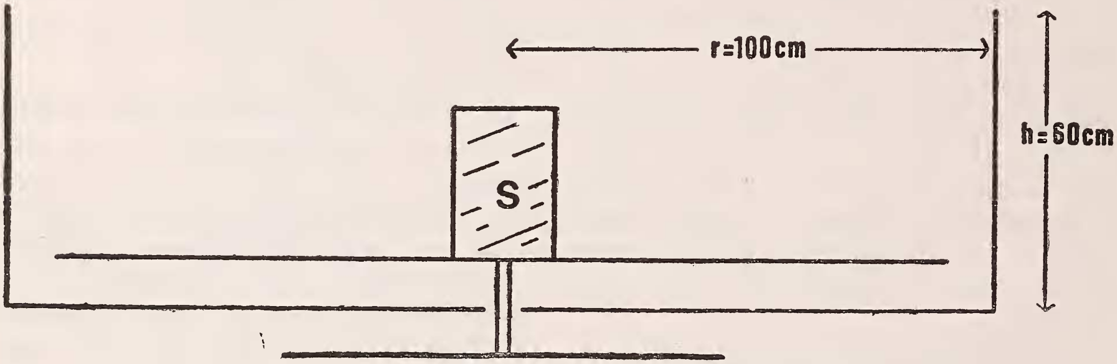

Fig. 1. Optomotor apparatus with rotating drum and fixed stand. S = snake in glass cage.

Back home I could obtain black-white paper stripes of 2 mm (=12′10″), 1 mm (=6′05″), and 0.5 mm (=3′03″). Intermediate angular presentations were realised by shifting the normally central position of the test animals' glass cage towards the periphery of the revolving drum, i.e. closer to the striped pattern. The reactions of the test animal consisted in:

(i) moving the whole body in the same direction as the revolving drum,

(ii) moving its anterior body portion or its head only,

(iii) eye movements only.

The number of such eye movements per time unit was noted down and proved to be nearly constant in each species under given conditions.

The revolving speed of the striped patterns must not exceed a certain angular velocity to make sure that true optomotor reactions can occur. Above that critical velocity, single visual events (i.e. stripes) cannot properly be separated and tend to blur resulting in a sort of flicker-fusion frequency effect. As stated above, visual acuity is affected by illumination level also. Brightness in my experiments in Madras ranged from 300 to 4,800 Lux and from 20 to 150 Lux in Münster, and there was no noticeable influence of illumination levels in this range on the visual acuity.

Of the 10 species tested in this manner, 6 yielded quantitative data, a survey of which is presented in the Table 3.

It may be mentioned that the behaviour of *Amphiesma stolata* was especially suited for the experimental procedure as their reactions were prompt and easily discernible. On the other hand, the rat snake (*Ptyas mucosus*) proved much less readily adapted to the experi-

TABLE 3

VISUAL ACUITY OF THE TESTED SPECIES

| | |
|---|---|
| *Ptyas mucosus* (Rat snake): | 4′30″ |
| *Amphiesma stolata* (Striped keel-back): | <6′ |
| *Xenochrophis piscator* (Checkered keel-back): | 20′–40′ |
| *Cerberus rhynchops* (Dog-faced water snake): | <1°15′ |
| *Naja naja* (Cobra): | 5′30″ |
| *Echis carinatus* (Saw-scaled viper): | 12′ |

mental situation. This may also account for the fact, that occasionally the test animal would not directly respond to the moving stripes but only in a delayed reaction. Working with cobras, though they were rather difficult to handle, proved a sheer pleasure at the broad stripes: placed in their central observation glass house, they would immediately lift their hood and precisely follow the moving striped pattern. Hence, the recorded data were especially reliable and easy to interpret. In contrast, the optomotor reactions of the saw-scaled viper (*Echis carinatus*) were difficult to observe. This was due to their small body size and minute optomotor eye movements.

Apart from the species listed above, a number of other Indian snake species did not show any optomotor reactions at all. Even if offered very coarse corresponding to 10° and 20°, they did not react. The unsuccessfully tested species were the following:

*Elaphe helena*: 4
*Dendrelaphis tristis*: 8
*Ahaetulla nasutus*: 8
*Python molurus*: 1

The results obtained above should be viewed in comparison to vision in other animals, e.g. the saw-scaled viper's visual acuity equals that of the European lizard (*Lacerta agilis*), both attaining 12′. It is remarkable that this seminocturnal viper's visual acuity reaches the level of the truly diurnal lizard.

Cobras (5.5′) and rat snakes (4.5′) are endowed with a definitely better vision than the lizard mentioned, and in this respect they compare almost with song birds like blackbird and yellow bunting.

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